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Body size distribution in sympatric oribatid mites (Acari: Sarcoptiformes) from California pine litter

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With one figure

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1. Introduction

Decomposing vegetation in temperate forest ecosystems is characteristically inhabited by a large number of small invertebrate species. In most coniferous forests the continual shedding of needles that are initially refractory to decomposers leads to the formation of a litter, or duff layer above the mineral soil, which exhibits a downward gradient of decomposition and is thoroughly penetrated by fungal mycelia. Within this latticework of decomposing needles and fungi feeds a very diverse assemblage of microarthropods dominated in both numbers of individuals and in species by a group of saprophagous mites, the Oribatida (Cryptostigmata).

Within a restricted litter type, several scores of oribatid mite species are commonly represented, with pooled densities reaching hundreds of thousands per square metre. Despite a multitude of studies which demonstrate some degree of feeding specificity in laboratory cultures, gut content analyses of field-collected specimens indicate that there is broad trophic overlap among sympatric species (MITCHELL & PARKINSON 1976, ANDERSON 1975a, BEHAN & HILL 1978). Because of this, we can think of oribatid mites as constituting a guild (ROOT 1967) which similarly utilizes the decomposing litter and associated microflora; the suggestion that they exploit this resource differently than their nearest major microarthropod guild, the Collembola, has been made by CROSSLEY (1977). This overlap does not preclude general trophic patterns within oribatid mite guilds. ANDERSON (1975a) has demonstrated that gut contents of field-collected specimens are roughly related to body size in that as size decreases, proportionally less decomposing higher plant material and more fungal material is included in the diet.

Mathematical relationships between body size and the partitioning of food resources within guilds of particulate feeders have been suggested for a wide variety of animals, especially predators, and especially from the standpoint of minimum similarity consistent with coexistence in competitive situations. Although both the theoretical and statistical validity of many such claims have been questioned (WILSON 1975, SIMBERLOFF & BOECKLEN 1981), the presence of real, non-random patterns would suggest, or at least be consistent with, the presence of deterministic biological interactions influencing the community structure of soil arthropods. The objectives of this study were to identify patterns of body size distribution in an oribatid mite guild and to discuss their possible significance.

2. Materials, methods, and sites

Native Monterey pine forests (*Pinus radiata* D. DON.) represent unique habitats with a high degree of plant endemism (VOGL *et al.* 1977). They presently occur as three disjunct stands along the coast of California near Año Nuevo, Monterey, and Cambria and are remnants of a once continuous forest on the outer coastal strip during the late Pleistocene, which was broken up by the coastward spread of warmer-drier climate during the Xerothermic Period (AXELROD 1977).

Table 1. Mean body length of 46 species of oribatid mites from *Pinus radiata* D. DON. needle litter at Jack's Peak, Monterey Co., California

| Species | Mean length (in μm) | Ratio com- pared to next smaller species | Species | Mean length (in μm) | Ratio com- pared to next smaller species |
|--|------------------------------------|---|---|------------------------------------|---|
| <i>Liochthonius</i> sp. | 180 | — | <i>Rhynchobelba</i> sp. | 371 | 1.03 |
| <i>Protoplophora palpalis</i> BERLESE | 180 | 1.00 | <i>Banksinoma spinifera</i> (HAMMER) | 380 | 1.02 |
| <i>Quadroppia quadricarinata</i> (MICHAEL) | 186 | 1.03 | <i>Oribatella</i> sp. | 388 | 1.02 |
| <i>Suctobelbella</i> sp. | 193 | 1.04 | <i>Gemmazetes</i> sp. cf. <i>clavatus</i> (JACOT) | 390 | 1.01 |
| <i>Cultroribula bicultrata</i> (BERLESE) | 210 | 1.09 | <i>Oppiella</i> sp. C | 402 | 1.03 |
| <i>Eobrachychthonius</i> sp. | 239 | 1.14 | <i>Scheloribates</i> sp. D | 407 | 1.01 |
| <i>Suctobelbella</i> sp. B | 240 | 1.00 | <i>Epidamaeus</i> (<i>Akrodamaeus</i>) sp. B | 424 | 1.04 |
| <i>Hungarobelba</i> sp. | 240 | 1.00 | <i>Ceratozetes</i> sp. | 440 | 1.04 |
| <i>Oppia</i> sp. | 249 | 1.04 | <i>Microtritia paeneminima</i> (WALKER) | 440 | 1.00 |
| <i>Cosmochthonius lanatus</i> (MICHAEL)* | 254 | 1.02 | <i>Metrioppia</i> sp. | 465 | 1.06 |
| <i>Oppiella nova</i> (OUDEMANS) | 256 | 1.01 | <i>Eremaeus magniporus</i> WALLWORK | 474 | 1.02 |
| <i>Lepidozetes trifolius</i> (FUJIKAWA) | 278 | 1.09 | <i>Propelops canadensis</i> (HAMMER) | 477 | 1.01 |
| <i>Minunthozetes</i> ? sp. | 280 | 1.01 | <i>Oribatella</i> sp. A | 488 | 1.02 |
| <i>Sphaerochthonius</i> sp. | 290 | 1.04 | <i>Anachipteria</i> sp. | 490 | 1.00 |
| <i>Aphelacarus acarinus</i> (BERLESE) | 290 | 1.00 | <i>Scheloribates</i> sp. C | 505 | 1.03 |
| <i>Beklemishevia galeodula</i> ZACHVATKIN | 296 | 1.02 | <i>Rhynchobelba</i> sp. A | 517 | 1.02 |
| <i>Oppiella</i> sp. B | 308 | 1.04 | <i>Plateremaeus</i> sp. | 523 | 1.01 |
| <i>Tectocephus velatus</i> (MICHAEL) | 310 | 1.01 | <i>Scheloribates</i> sp. A | 575 | 1.10 |
| <i>Epidamaeus</i> (<i>Akrodamaeus</i>) sp. C | 312 | 1.01 | <i>Epidamaeus</i> (<i>Akrodamaeus</i>) sp. D | 590 | 1.03 |
| <i>Joshuella striata</i> WALLWORK | 320 | 1.03 | <i>Trhypochthonius americanus</i> (EWING) | 595 | 1.01 |
| <i>Scheloribates</i> sp. B | 336 | 1.05 | <i>Eupelops</i> sp. | 613 | 1.03 |
| <i>Lepidozetes</i> sp. B | 338 | 1.01 | <i>Hermanniella</i> sp. | 693 | 1.13 |
| <i>Zachvatkiniabates</i> sp. | 361 | 1.07 | <i>Galumna</i> sp. | 712 | 1.03 |

*) n. comb.

During a two year period, 200 rectangular cores (30 cm²) of decaying needles were taken from the largest native stand of Monterey pine located near Monterey at Jack's Peak Regional Park. At Año Nuevo, the northernmost native stand, 99 cores were taken at the Coastways Ranch. In addition, in Contra Costa County, north of the natural range of Monterey pine, 80 cores were taken in a plantation of 35 year old trees near San Pablo Dam. All cores were taken to the humus-mineral soil interface at 0.5 m from the base of dominant or codominant trees of Monterey pine in closed stands with no significant undergrowth.

Microarthropods were extracted from these cores into ethanol using a Tullgren high gradient extractor. Oribatid mites were sorted from these collections. Measurements of total body length in 10 micrometer classes were made ventrally on slide mounted mites previously cleared in lactophenol. Since a slight sexual size dimorphism usually exists, and abundances are rarely equal, the average length for a species was calculated as the mean of the average length of males and the average length of females. Some species are all female (parthenogenetic).

3. Results

Over 20,000 oribatid mites representing 85 species were extracted from the 379 cores taken at the three sites. The guilds of the two native stands at Año Nuevo and Jack's Peak shared about 70% of their species, but the plantation at San Pablo Dam was strongly dissimilar, sharing about one-third (with Jack's Peak) to one-fifth (with Año Nuevo) of the native stands' species. All three exhibited broad taxonomic and size ranges indicated for the Jack's Peak fauna in Table 1.

The mean body length of the species listed in this table is 381 μ m; the median value is 361 μ m (*Zachvatkinibates* sp.), so the distribution is not substantially skewed. Size ratios between a given taxon and that taxon above it in the table range from 1.00 to 1.14 with all but three values less than 1.10 and 38 (83%) less than 1.05. From visual inspection it is clear that no minimum similarity limit, with regard to body size, is manifested in this oribatid mite guild.

Alternatively we can restrict our approach and examine only closely related taxa, congeners in particular. If the body length displacement within all encountered pairs of sym-

Table 2. Mean body lengths (in μ m, \pm standard deviation) and ratios for (N) adult specimens of sympatric oribatid mite congeners from California *P. radiata* litter

| Species | Jack's Peak | Año Nuevo | San Pablo | Larger: smaller congener |
|--------------------------------------|--------------------|--------------------|-------------------|--------------------------------|
| <i>Oppiella nova</i> (OUDEMANS) | 256 \pm 14 (50) | 257 \pm 10 (31) | 272 \pm 14 (23) | |
| <i>Oppiella</i> sp. B | 308 \pm 20 (37) | — | — | 1.20 |
| <i>Oppiella</i> sp. C | — | 334 \pm 16 (51) | — | 1.30 |
| <i>Oppiella</i> sp. D | — | — | 340 \pm 8 (27) | 1.25 |
| <i>Rhynchobelba</i> sp. B | 371 \pm 17 (14) | — | — | |
| <i>Rhynchobelba</i> sp. A | 517 \pm 22 (25) | — | — | 1.39 |
| <i>Suctobelbella</i> sp. A | 193 \pm 11 (48) | 191 \pm 14 (11) | — | |
| <i>Suctobelbella</i> sp. B | 240 \pm 14 (66) | 241 \pm 11 (21) | — | 1.24, 1.26 |
| <i>Eremaeus</i> sp. B | 535 \pm 24 (15) | — | — | |
| <i>Eremaeus stiktos</i> HIGGINS | 662 \pm 25 (58) | — | — | 1.24 |
| <i>Joshuella</i> sp. A | — | — | 293 \pm 11 (27) | |
| <i>Joshuella striata</i> WALLWORK | — | — | 370 \pm 13 (24) | 1.26 |
| <i>Epidamaeus</i> sp. E*) | — | 285 \pm 13 (33) | — | |
| <i>Epidamaeus</i> sp. A | — | 383 \pm 18 (77) | — | 1.38 |
| <i>Epidamaeus</i> sp. C | 312 \pm 13 (26) | — | — | |
| <i>Epidamaeus</i> sp. B | 424 \pm 25 (33) | — | — | 1.36 |
| <i>Oribatella</i> sp. B | — | — | 388 \pm 12 (12) | |
| <i>Oribatella</i> sp. A | — | — | 488 \pm 12 (15) | 1.26 |
| <i>Lepidozetes trifolius</i> (F.) | 278 \pm 12 (104) | 276 \pm 11 (111) | — | |
| <i>Lepidozetes</i> sp. B | 338 \pm 12 (77) | 342 \pm 14 (18) | — | 1.21, 1.24 |

*) All *Epidamaeus* species collected belong to the subgenus *Akrodamaeus*.

patric congeners (except in *Scheloriates*) is calculated (Table 2) the ratio of larger to smaller congener is remarkably consistent, 1.2 to 1.4. For example, *Oppiella nova* (OUDEMANS), a cosmopolitan parthenogenetic species, co-occurred at each site with a different undescribed species of *Oppiella* with ratios between 1.2 and 1.3. Different pairs of species of *Epidamaeus*, a genus which has undergone an extensive radiation in Western North America, were represented at the two native stands, with each pair exhibiting almost identical size differences. A rare fifth species (*Epidamaeus* sp. D) was present at Jack's Peak and Año Nuevo sites in very low numbers (pooled $n = 5$, $\bar{x} = 500 \mu\text{m}$), and its size ratios with *Epidamaeus* sp. B and sp. A are 1.39 and 1.50 respectively.

In addition to the congeneric pairs in Table 2, a four-congener sequence in the genus *Scheloriates* was present at Jack's Peak (Figure 1). The regular spacing of sizes noted above is represented in this genus on an extended scale, with only one ratio (sp. A : sp. C) dropping somewhat below 1.2. Is this significant? Given these four sympatric congeners and three

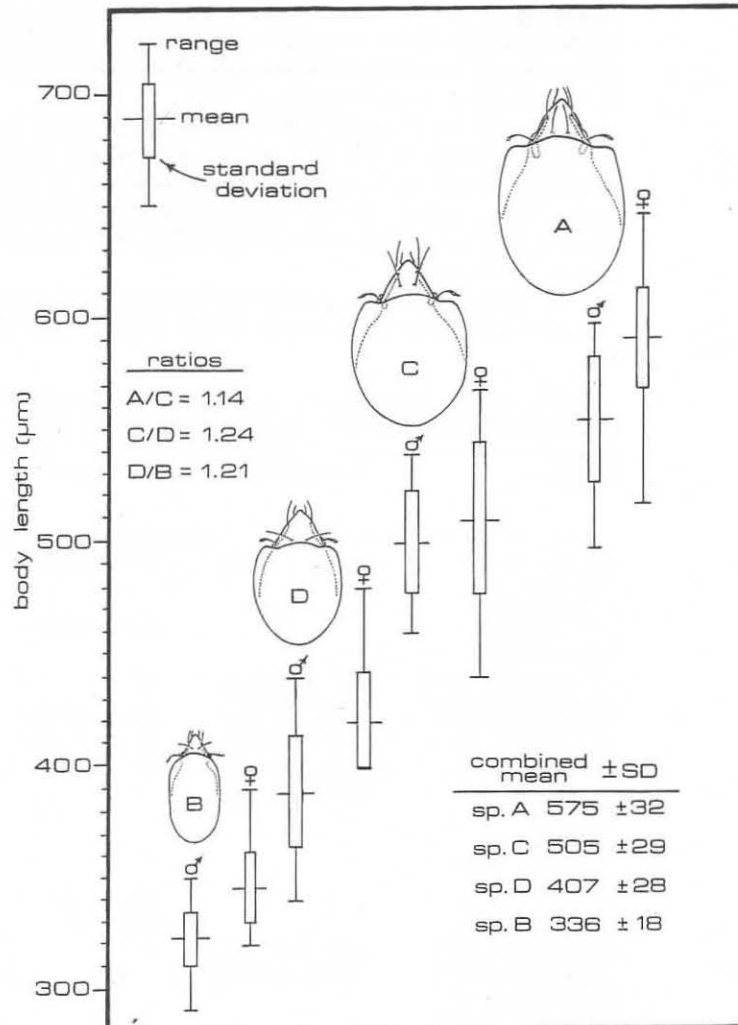


Fig. 1. Distribution of body length for four species of *Scheloriates* from Jack's Peak, Monterey California. See text for method of calculating combined means (sp. A, ♀ $n = 54$, ♂ $n = 60$; sp. B, ♀ $n = 72$, ♂ $n = 58$; sp. C, ♀ $n = 22$, ♂ $n = 31$; sp. D, ♀ $n = 16$, ♂ $n = 13$).

observed size ratios, we can pose the hypothesis that the minimum observed ratio (1.14) could be expected if the sizes of the two intermediate species were determined at random, within the bounds established by the smallest and largest. SIMBERLOFF & BOECKLEN (1981) proposed a test for such a hypothesis in which the ratios are expressed as lengths of segments along a unit line (differences in logarithms). Given n ratios, the probability that random placement of $n - 1$ points along this line would yield a minimum segment (g_1) which is smaller than the observed minimum segment (a) is calculated as:

$$\Pr(g_1 < a) = 1 - (1 - na)^{n-1}$$

Our series of *Scheloribates* spp. body lengths (in μm) is 336, 407, 505, 575 (Figure 1); taking natural logarithms allows us to express their respective ratios as three linear distances (differences between successive logarithms), which are 0.192, 0.216, 0.129. These are proportionally scaled to a unit line by multiplying by a constant (1.89), and become 0.358, 0.402, 0.240. When our minimum observed differences (representing the minimum ratio) are applied to the above equation ($a = 0.24$, $n = 3$), the result is a probability of 0.922 that random assignment of the intermediate species' sizes would give a minimum ratio smaller than that observed. The expected minimum size of an equal number of randomly produced segments on a unit line is $1/n$, or 0.11 (SIMBERLOFF & BOECKLEN 1981), half the size of the observed, and we can reasonably reject our hypothesis. The minimum observed ratio was probably not randomly determined.

Scheloribates spp. *B* and *C* are also present at Año Nuevo, where they form a congeneric pair (spp. *A* and *D* are absent). Here sp. *B* has a mean length of $356 \mu\text{m}$ (± 22 , $n = 16$) and sp. *C* has a mean length of $434 \mu\text{m}$ (± 22 , $n = 37$). These differ from the respective mean lengths of the populations at Jack's Peak where sp. *C* is 16.4% larger and sp. *B* is 5.6% smaller. Whereas the size ratio of sp. *C*: sp. *B* is 1.50 at Jack's Peak, it is 1.22 at Año Nuevo. The possible significance of the intermediate-sized sp. *D* at Jack's Peak will be discussed below.

4. Discussion

HUTCHINSON's (1959) classic question "why are there so many kinds of animals?" becomes even more perplexing when considering the small species represented in great abundance in the principal heterotrophic subset of most terrestrial communities, the soil and litter. Of great importance in answering this question is knowledge of the role of competition in determining species diversity. In mature temperate forests, where usually a large majority of primary production flows through decomposer food webs in the soil system, there is no evidence of widespread overabundance of food resources, since there is no long-term net accumulation of organic matter (SLOBODKIN *et al.* 1967). However, as ANDERSON (1975b) has indicated, this does not necessarily implicate food as a limiting resource in the population dynamics of saprophagous soil animals. In addition to seasonal inequality in litter input, substantial annual variation is not uncommon, especially in coniferous forests (BRAY & GORHAM 1964). When combined with short term changes in wind patterns and topographic irregularities, the resulting pattern of organic matter deposition is far from equitable; it forms an unpredictable mosaic in time and space (ANDERSON 1973, MITCHELL 1978). Continuous and widespread exploitation competition among saprophagous soil animals is unlikely (ANDERSON & HEALEY 1972) and one might predict that competition-mediated food partitioning is not the rule.

Based on general lack of such partitioning as noted above the oribatid mite guild appears to follow this prediction. Also, based on the minimum similarity theory of HUTCHINSON (1959) we might expect to find size ratios in the 1.2 to 1.4 range to be the rule if food competition were significant; in fact no such general pattern is suggested by the data.

WIENS (1977) has suggested that competition-based models of species diversity are generally overemphasized; environmental variation and other factors may often be effective in keeping densities below critical levels. Although soil is often cited as a relatively stable environment, the upper layers, particularly the litter, can experience considerable seasonal

temperature and humidity variation which may impact (either directly as agents of mortality, or indirectly as determinants of feeding and reproductive activity) on oribatid mite densities.

The model suggested by MENGE & SUTHERLAND (1976) would also predict a minor role for competition in oribatid mite guilds. They suggest that diversity in animals of lower trophic levels is more likely to be controlled by predation. Also, as part of a highly complex system of many trophic levels a prediction of predator controls is reinforced. The actual impact of natural enemies on oribatid mite densities remains to be determined, but there is no reason to consider it insignificant. It is probably concentrated most in the soft-bodied immature instars; adults of most species are heavily sclerotized but they are still susceptible to predaceous beetles, the larger of the predaceous mites and others. Sporozoan parasites are also now becoming recognized as abundant and perhaps significant agents of mortality (PURRINI 1983).

If on the other hand, competition for food were overriding, an alternative explanation for the absence of a lower limit to size similarity in the oribatid mite guild as a whole might be proposed. As particulate feeders, and as small members of a trophic level which includes millipedes, earthworms and other large invertebrates, oribatid mites might be expected to follow the general model of WILSON (1975), who suggested that such characteristics are less likely to promote patterns of minimum similarity. Assuming that the unknown "success-of-capture curve" in this trophic level is similar to that of other particulate feeders, the guild as a whole fits this model; large size ratios are absent from Table 1. Larger oribatid mites utilize a wider range of food types (ANDERSON 1975a) probably because the fragmentation of higher plant structural material requires more substantial size and power than does feeding on fungal hyphae or spores. Consequently, the xylophages, phyllophages and panphytophages listed by LUXTON (1972) are principally larger mites. Since larger size does seem to bestow some feeding advantage, the guild could theoretically represent a competitive gradient as conceived by WILSON (1975).

That competitive interactions are possible between two related oribatid mites has been nicely demonstrated by ANDERSON (1978a), who noted considerable shifts in utilization of food and space by mixed populations, compared to single species populations, in laboratory microcosms. The possibility was reiterated that "competition for resources does occur, but . . . the 'dynamic mosaic' nature of soil and litter microhabitats in space and time and the microhabitat specificity of many species . . . restricts competitive exclusion to local patches and to short time periods".

If food competition is operative only intermittently among soil saprophages, with natural enemies and environmental variation presumably controlling densities and diversity at other times (ANDERSON 1975b, CONNELL 1975, WIENS 1977), why do we see limits to size similarity between congeneric pairs which seem to nicely fit Hutchinson's rule by having ratios consistently between 1.2 and 1.4? A linear ratio of 1.2 implies a doubling of volume (or mass) for animals of similar body shape (HUTCHINSON 1978), so for small animals inhabiting forest litter differences in size may have considerable ramifications. There are several advantages to being larger. One is the availability of a wider range of food as discussed above, and the concomitant advantage of opportunistic feeding, which large oribatid mites have been shown to exhibit (ANDERSON 1975a). Larger size also entails a smaller surface to volume ratio and less susceptibility to desiccation. In general, larger animals invest less in reproduction in relation to body weight (BLUEWISS *et al.* 1978).

Being smaller has its own advantages. Possibly most significant is access to more and a greater variety of spaces in the litter environment. A litter layer is an extremely complex and strongly three dimensional matrix of microhabitats for organisms the size of oribatid mites. Few habitats, if any, have greater possible structural diversity. Since they are not burrowing organisms, access to many spaces is denied the larger species. Whether the space be a potential feeding site in times of food competition or a refuge site to avoid predation, the small animal may be more successful. Habitat structure may also affect the foraging efficiency of predators and it has been suggested that the indirect influences of habitat

structure may be more an important influence on diversity than factors directly related to food (SCHOENER 1974, MENGE & SUTHERLAND 1976).

That observed body size differences in closely related sympatric animals can be due to factors other than food particle size has already been suggested. Behavioral differences in congeneric gastropods (LEVINTON 1982) and differences in microhabitat utilization in a guild of spider crabs (HINES 1982) may relate to body size. In oribatid mites a relationship between habitat structural diversity and species diversity has been demonstrated (ANDERSON 1978b). It is not unreasonable to suggest that the differences observed here between sympatric congeners might relate to space utilization.

DARWIN (1859) long ago noted that species in the same genus, which are morphologically and often behaviorally similar, are most likely to exhibit intense competition when thrown together. On the one hand, congeners are nearest neighbors in morphological space because of shared genetic heritage, and on the other hand this similarity puts sympatric congeners under pressure to diverge in the utilization of resources (KARR & JAMES 1975). The data for the four species of *Scheloribates* suggest character displacement in the form of size divergence, with the driving interaction possibly relating to habitat space. Although we have no allopatric population of *Scheloribates* sp. *D*, the size displacement of sp. *C* from allopatry at Año Nuevo to sympatry with sp. *D* at Jack's Peak is striking (that of sp. *B* is less so). As a result, whether one compares the two species at Año Nuevo (*B*, *C*) or the three at Jack's Peak (where sp. *D* is intermediate between spp. *B* and *C*) the size ratios are all 1.2.

In conclusion, size patterns do exist in a guild of oribatid mites, but they exhibit a limiting similarity in size only between congeners. As WIENS (1982) stated, such patterns in no way validate claims of deterministic biological interactions between taxa, but their discovery in oribatid mites raises interesting problems. The generalized nature of oribatid feeding habits make it unlikely that the consistent differences in body size among sympatric congeners is entirely associated with food-resource partitioning. Although competitive interactions necessary for partitioning have been demonstrated in the laboratory (ANDERSON 1978a) it is not clear that competitive situations are widespread or frequent in the soil system. Since the consistent size difference between sympatric congeneric species of oribatid mites does suggest that a biological factor is involved, the current emphasis on exploitation competition as a mechanism for structuring communities may be misplaced.

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The oribatid mite guild of decomposing Monterey pine litter at three California locations was examined for salient patterns of body size (total length) distribution, especially searching for minimum limits to similarity between taxa. When representatives of all sympatric species were considered, no minimum size ratio was discernable, but when only sympatric congeners were compared, body size ratios (larger: smaller) were mostly in the range 1.2—1.4, consistent with the Hutchinson model of minimum similarity. A possible example of character displacement in *Scheloriobates* is discussed, and it is suggested that observed body size patterns may reflect interspecific interactions in habitat-space utilization, rather than having resulted from competition-mediated food partitioning.

Key words: Oribatei, mites, competition, minimum similarity, Monterey pine, body size.